Superbiflorae by the pilose indument on the twigs, leaves, and inflorescences axes and by the reflexed corolla lobes. *Cordia pilosa* is closely related to *C. superba* Cham. and *C. rufescens* A. DC., sharing the large flowers (greater than 3 cm long). However, *C. superba* differs from *C. pilosa* by its indument that is scabrous with strigose hairs or often glabrescent, but never pilose, and by the spreading corolla lobes; *C. rufescens* can be distinguished from *C. pilosa* by its villous indument and smaller corolla (3.0–3.5 cm). *Cordia pilosa* appears to be distylous, as reported in other species of *Cordia* (Taroda & Gibbs, 1986).

Paratypes. BRAZIL. **Alagoas:** Limoeiro de Anadia, 11 June 1981, *A. D. Andrade-Lima, R. Pereira & A. Du Bocage 75* (HUEFS); Barra de São Miguel, 25 Mar. 1986, *R. P. Lyra-Lemos & G. L. Esteves 1190* (HUEFS, MAC); Penedo, 14 Nov. 1985, *R. P. Lyra-Lemos & A. T. L. Pinheiro 1103* (HUEFS, MAC); Coruripe, Colônia de Pindorama, 21 Oct. 1998, *R. P. Lyra-Lemos & M. N. Rodrigues 3979* (HUEFS, MAC); Piaçabuçu, Tapera, 22 Oct. 1987, *I. S. Moreira, G. L. Esteves, R. P. Lyra-Lemos, R. S. Nascimento & A. F. L. Pinheiro 59* (HUEFS, MAC); Campo Alegre, Faz. Matão, 25 Nov. 1997, *M. N. Rodrigues, R. P. Lyra-Lemos & J. Santinho 1174* (HUEFS, MAC). **Bahia:** Entre Rios, 11°53′08″S, 37°57′13″W, 25 Feb. 2005, *J. G. Carvalho-Sobrino & A. C. Assunção 347* (HUEFS); São Sebastião do Pessé, Faz. Panema 12°33′S, 38°23′W, 27 Mar. 2001, *G. Carvalho et al. 21* (ALCB); Conde, 30 km from Conde, 25 Mar. 1995, *F. França & E. Melo 1145* (HUEFS); Itanagra, Faz. Brejo Verde, 26 Oct. 1975, *E. F. Gusmão 375* (ALCB); Conceição do Jacuipe, Rio Pojuca, 12°32′S, 39°05′W, 7 Mar. 2003, *M. V. Moraes 575* (HUEFS); Entre Rios, rd. to Imbé, 12°7′40″S, 37°59′14″W, 20 Jan. 2007, *T. S. Nunes, N. K. R. Souza & K. T. R. Souza 1767* (HUEFS); Mata de São João, praia Malhada, 12°30′37″S, 38°00′36″W, 18 Nov. 2005, *A. K. A. Santos, S. F. Conceição & T. S. Nunes 468* (HUEFS); Entre Rios, rd. Conde–Esplanada, 11°45′17″S, 37°45′45″W, 23 Jan. 2004, *M. Stapf 201* (HUEFS, SJRP), *M. Stapf 202* (HUEFS), *M. Stapf 203* (HUEFS), *M. Stapf 204* (HUEFS), 3 Feb. 2004, *M. & D. Stapf 229* (HUEFS, SJRP). **Sergipe:** Indiaroba, rd. to Pontal, ca. 1 km from hwy. SE 100, 11°28′57″S, 37°27′37″W, 19 Aug. 2003, *K. R. B. Leite & A. S. Conceição 337* (HUEFS).

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Review of New World *Alfaroa* and Old World *Alfaropsis* (Juglandaceae)

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Abstract. *Alfaroa* Standl. has five species with a total of 10 taxa ranging from southern Mexico to northern Colombia, although Costa Rica has the most (four), including the type species *A. costaricensis* Standl. A taxonomic treatment of the Juglandaceae for *Flora Mesoamericana* recognizes the new subspecies *A. costaricensis* subsp. *septentrionalis* D. E. Stone from Mexico and Guatemala as a northern variant. Review of *A. guanacastensis* D. E. Stone reduces the species to synonomy under *A. manningii* J. León. The widespread southeastern Asian genus *Alfaropsis* Iljinsk. (= *Engelhardia roxburghiana* Wall.) is monotypic while possessing several morphological and molecular characters somewhat intermediate between New World *Alfaroa* and *Oreomunnea* Oerst., on the one hand, and Old World *Engelhardia* Lesch. ex Blume on the other. Although *Alfaropsis* was proposed in 1993, the generic name was not generally recognized until the phylogeny of extant and fossil Juglandaceae was examined by Manos et al. in 2007.

Key words: *Alfaroa*, *Alfaropsis*, *Engelhardia*, IUCN Red List, Juglandaceae, *Oreomunnea*.

The latest taxonomic treatment of the Juglandaceae provisionally recognized 10 genera in two subfamilies (Manos & Stone, 2001: table 1): Engelhardioideae, which contains *Alfaropsis* Iljinsk. and *Engelhardia* Lesch. ex Blume from the Old World and *Alfaroa* Standl. and its sister genus *Oreomunnea* Oerst. in the New World; and the Juglandoideae, including *Platycarya* Siebold & Zucc., *Cyclocarya* Iljinsk., *Pterocarya* Kunth, and *Annamocarya* A. Chev. (probably best recognized as section *Rhamphocarya* W. E. Manning & Hjelmq. of the genus *Carya* Nutt. [Manning & Hjelmqvist, 1951]) found extant only in the Old World, and *Carya* and *Juglans* L. occurring in both the New and Old World (Manning, 1978; Manchester, 1987). Because of the distinctive, fossilizable fruit, another nine or so genera are known from the fossil record dating back to the early Eocene (Manchester, 1987). Of the extant genera, however, *Alfaroa* is the only member not represented in the fossil record, although pollen of the *Alfaroa–Oreomunnea* clade is known from Mesoamerica (Graham, 1976, 1985).

The most recent taxonomic assessment of *Alfaroa* (Stone, in press) recognizes five species, four subspecies, and one putative hybrid (*A. costaricensis* Standl. × *A. williamsii* Ant. Molina = *A. costaricensis* var. *elongata* W. E. Manning [Stone, 1977; Morales, 2007]): *A. costaricensis* (with subspecies *costaricensis* and *septentrionalis* D. E. Stone), *A. guatemalensis* (Standl.) L. O. Williams & Ant. Molina, *A. manningii* J. León, *A. mexicana* D. E. Stone, and *A. williamsii* (with subspecies *williamsii* and *tapantiensis* D. E. Stone) (Table 1). The type species of the genus, *A. costaricensis*, was described by Paul C. Standley from El Muñeco in Costa Rica as "perhaps the richest locality botanically that I have ever seen" (Standley, 1927: 77). The trees reached canopy status in the moist, premontane rainforests that once were, but they are also quite capable of flowering and fruiting when mere shrubs or at least subcanopy trees. While *Alfaroa* and *Oreomunnea* are distinctive in the family because of their compound leaves that have opposite phyllotaxy, the type species stands apart from other species of *Alfaroa* because of its short, almost obsolete petioles (0.4–2[–3] cm), very small lowermost leaflets (less than one third the length of the longest), and above all a hirsute pubescence that covers the petiole, rachis, abaxial leaflet surface, and the moderate-sized (2–3 cm) fruit that is superficially walnut-like. The typical *A. costaricensis* subsp. *costaricensis* (Fig. 1) is found in the mountains of Costa Rica and Panama, but a close congener known from a few collections in Mexico and Guatemala is described here as a new subspecies. It should be noted that this taxon has not been found in Honduras and Nicaragua, even though each of these intervening countries has a representative of the genus.

A New Subspecies of *Alfaroa costaricensis*

1. Alfaroa costaricensis Standl., J. Wash. Acad. Sci. 17(4): 78. 1927. TYPE: Costa Rica. Cartago: in moist forests at El Muñeco, S of Navarro, ca. 1400 m, 8 Feb. 1924, *P. C. Standley 33620* (holotype, US 1226388).

1a. Alfaroa costaricensis subsp. **costaricensis**.

1b. Alfaroa costaricensis subsp. **septentrionalis** D. E. Stone, subsp. nov. TYPE: Guatemala.

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Table 1. Distinguishing features of six closely related taxa of *Alfaroa*.

Character	*A. costaricensis* subsp. *costaricensis*[1]	*A. costaricensis* subsp. *septentrionalis*[2]	*A. guatemalensis*[3]	*A. manningii*[4]	*A. mexicana*[5]	*A. williamsii*[6]
Distribution	Costa Rica, Panama	Mexico, Guatemala	Guatemala, Honduras, Mexico	Costa Rica	Guatemala, Mexico	Nicaragua, Costa Rica, Panama, Colombia
Basal pair leaflets	highly reduced	highly reduced	only slightly reduced	only slightly reduced	only slightly reduced	moderately reduced
Petiole:						
length	short (0.4–2[–3] cm)	short (0–1[–2.5] cm)	long (3.5–7 cm)	long (2–9 cm)	long ([2.5–]3–4[–10] cm)	variable ([1.5–]2–5[–7] cm)
hairs	densely hirsute	lightly hirsute	glabrous	glabrous	glabrous	glabrous
Rachis	densely hirsute	lightly hirsute	glabrous	glabrous	glabrous	glabrous
Petiolule	absent to very short (0–1 mm)	absent to short (0–3 mm)	long (3–8 [–10] mm)	variable ([1–]2–5[–10] mm)	variable ([2–]5–8[–10] mm)	short (1–3 mm)
Abaxial leaflet surface:						
pubescence	yes	no	no	no	clustered at base	no
revolute at base	sometimes	no	no	sometimes	yes	no
peltate scale density	sparse	sparse	dense	dense	dense	moderate
Leaflet base	truncate or rounded	obliquely tapering	wedge-shaped to rounded	wedge-shaped to rounded	wedge-shaped to rounded	tapering or rounded
Male flower pedicel	long	unknown	obsolete	obsolete	obsolete	± sessile
Female flowers	hirsute	glabrous to lightly hirsute	glabrous	glabrous	glabrous	glabrous
Fruit	hirsute	glabrous	glabrous	glabrous	glabrous	glabrous

[1] Standley, 1927.
[2] This paper.
[3] Williams and Molina, 1970.
[4] León, 1953.
[5] Stone, 1968.
[6] Molina, 1968.

Quetzaltenango: 14°43′N, 91°31′W, 1600 m, 17 May 1966, *D. E. Stone 2210* (holotype, DUKE; isotype, MO). Figure 2.

Haec subspecies ab *Alfaroa costaricensi* Standl. subsp. *costaricensi* foliorum petiolo rachideque parce (vs. dense) hirsutis, petiolulis 0–3 (vs. 0–1) mm longis, foliolis basi attenuatis usque rotundatis (vs. truncatis, rotundatis vel attenuatis) subtus in aetate omnino glabris, floribus femineis parce (vs. dense) hispidis atque fructu glabro (vs. dense hirsuto) distinguitur; etiam Mexico et Guatemala (vs. Costa Rica et Panama) habitat.

Trees or large shrubs evergreen, to 25 m tall and 70 cm DBH; buttresses small or absent; *bark* tight, lenticillate, reddish brown on exterior, pale yellow on interior; *wood* whitish on outer flanks; *pith* of previous year's growth solid; *terminal buds* unprotected by bud scales, though covered with hairs and peltate scales. *Leaves* compound, even-pinnate, opposite, occasionally whorled, or infrequently alternate; *petioles* 0–1 (–2.5) cm, lightly hirsute; *rachises* 10–15(–30) cm, lightly hirsute; leaflets 14 to 24, basal pair conspicuously reduced compared to the longest ones to < 1/3 the length, or often obscured or lost; *petiolules* sessile to 3 mm; blades obliquely tapered at base, flat, margins serrate on seedlings and saplings, entire or with occasional serrations on mature trees, both surfaces glabrous but with a light density of peltate scales abaxially, and sometimes glaucous adaxially. *Staminate inflorescences* terminal. Mature *staminate flowers* and *pollen* unknown. *Pistillate inflorescences* terminal. *Pistillate flowers* numerous along erect axis; *floral cup* without pedicel, 3-lobed bract and 2 fused bracteoles forming a low rim subtending 4 sepals fused below and a lightly hirsute *ovary*, peltate scales dense; *style* 1, long, bifurcate with deep clefts; *stigma* 2-parted, carinal orientation (stylar arms orthogonal to primary septum). *Fruit* a drupaceous nut, 8-chambered, sessile, ellipsoid to ovoid, ca. 3 × 2–2.5 cm;

Figure 1. Herbarium sheet of *Alfaroa costaricensis* subsp. *costaricensis* (*Stone 2174*, DUKE), from Costa Rica, with opposite phyllotaxy, sessile leaflets with revolute margins at base, and a terminal pistillate spike. Scale bar = 17.5 mm.

husks glabrous, or rarely with a few hairs, sometimes glaucous; *shell* + husk 1–2 mm, cartilaginous; *seed* germination hypogeal. *Seedlings* with first aerial leaves compound, serrate, opposite.

Distribution, habitat, and IUCN Red List category. *Alfaroa costaricensis* subsp. *septentrionalis* is known from southeastern Mexico (Chiapas, Veracruz) and western Guatemala (Huehuetenango, Quetzalte-

Figure 2. Holotype of *Alfaroa costaricensis* subsp. *septentrionalis* (*Stone 2210*, DUKE), from Guatemala, with opposite phyllotaxy, very short petiolulate leaflets showing only the slightest indication of revolute margins at base, and a terminal pistillate spike. Scale bar = 19.5 mm.

nango, Suchitepéquez). The Veracruz plants on Volcán Santa Marta are on the northeastern side of the Istmo de Tehuantepec and effectively isolated from the Mexican and Guatemalan highlands, where the other collections have been made. The trees occur on rich volcanic soil at 1300–1700 m in ecological conditions favorable for mountain-grown coffee, as is the case for a number of black walnut species (Stone et al., 2009). The current conservation status of this subspecies is unknown, and the IUCN Red List

Table 2. Comparison of *Alfaropsis* with its three closest relatives (Engelhardioideae). Based on Iljinskaya (1990, 1993), Manchester (1987), Manning (1949), Stone (1972), and Manos and Stone (2001).

	Alfaropsis	*Engelhardia*	*Alfaroa*	*Oreomunnea*
No. of species	1	4 to 8	5	2
Extant range	SE Asia	SE Asia	Latin America	Latin America
Habit	evergreen	deciduous	evergreen	evergreen
Phyllotaxy	alternate	alternate	opposite	opposite
Leaflet:				
base	flat	flat	sometimes revolute	sometimes revolute
margin	entire	entire/serrate[1]	entire (serrate)[2]	entire (serrate)
ultimate venation	open	open	closed	closed
rhombic crystals in parenchyma	absent	absent	present	present
abaxial surface:				
texture	flat	flat	papillose	papillose
stomata	surface	surface	sunken	sunken
Inflorescence:				
arrangement	androgynous panicle (separate)[3]	separate	androgynous panicle (separate)[3]	androgynous panicle (separate)[3]
position	terminal (lateral)[4]	lateral	terminal (lateral)[4]	terminal (lateral)[4]
location	new wood (old)[5]	old wood	new wood (old)[5]	new wood (old)[5]
Male flower:				
receptacle	rounded	elongate	rounded	rounded/elongate[6]
floral segments	2	2 to 4	4 to 7	2 to 4
pollen:				
size	14–15 μm	17–22 μm	20–26 μm	20–26 μm
wall	nexine thick	nexine thin	nexine thick	nexine thick
aperture	oblong to circular	elongate	oblong to circular	oblong to circular
Female flower:				
stigma:				
orientation	split carinal	commissural[7]	carinal[8]	carinal
shape	globose	elongate	globose	globose
style	lacking	elongate	lacking	lacking
bract	3-winged	3-winged	rudimentary	3-winged
wing venation	pinnate	pinnate	NA	triveined
bracteoles	proximal rim	proximal flap	rudimentary scale	proximal flap
cells at base	4	2(to 4)	8	8
cotyledons	entangled	entangled	separate	separate
germination	epigeal	epigeal	hypogeal	hypogeal
Phylogenetic affinities[9]	sister to *Oreomunnea* and *Alfaroa* clade	sister to all Engelhardioideae genera	sister to paraphyletic *Oreomunnea*	paraphyletic to *Alfaroa*

NA, data not available.
[1] Leaflets entire in some species; serrate in others.
[2] Leaflets mainly entire in adult plants; serrate in juveniles and sucker shoots.
[3] Mainly androgynous; sometimes separate.
[4] Mainly terminal on new wood; occasionally lateral, and if so on old wood.
[5] Mainly on new wood; occasionally on old.
[6] Compact and rounded in one species; elongate in the other.
[7] Stylar arms parallel to primary septum.
[8] Stylar arms orthogonal to primary septum.
[9] cpDNA/ITS (see Manos et al., 2007).

category is assessed as Data Deficient (DD) (IUCN, 2001). In 1952, however, Manning (1952: 354) noted that "the tree is plentiful in some regions...and...is particularly plentiful in the mountain forest along the old road between Finca Pirineos and Patzulín, Quezaltenango"; I found this to still be true in 1971. However, one cannot be sanguine about the conservation of any plant that has similar ecological requirements to a commercial crop such as coffee. This is particularly true in Guatemala where forests covered 65% of the total land area in 1950, but only 26% remained forested in 2000. As Loening and Sautter (2005: 393) have noted

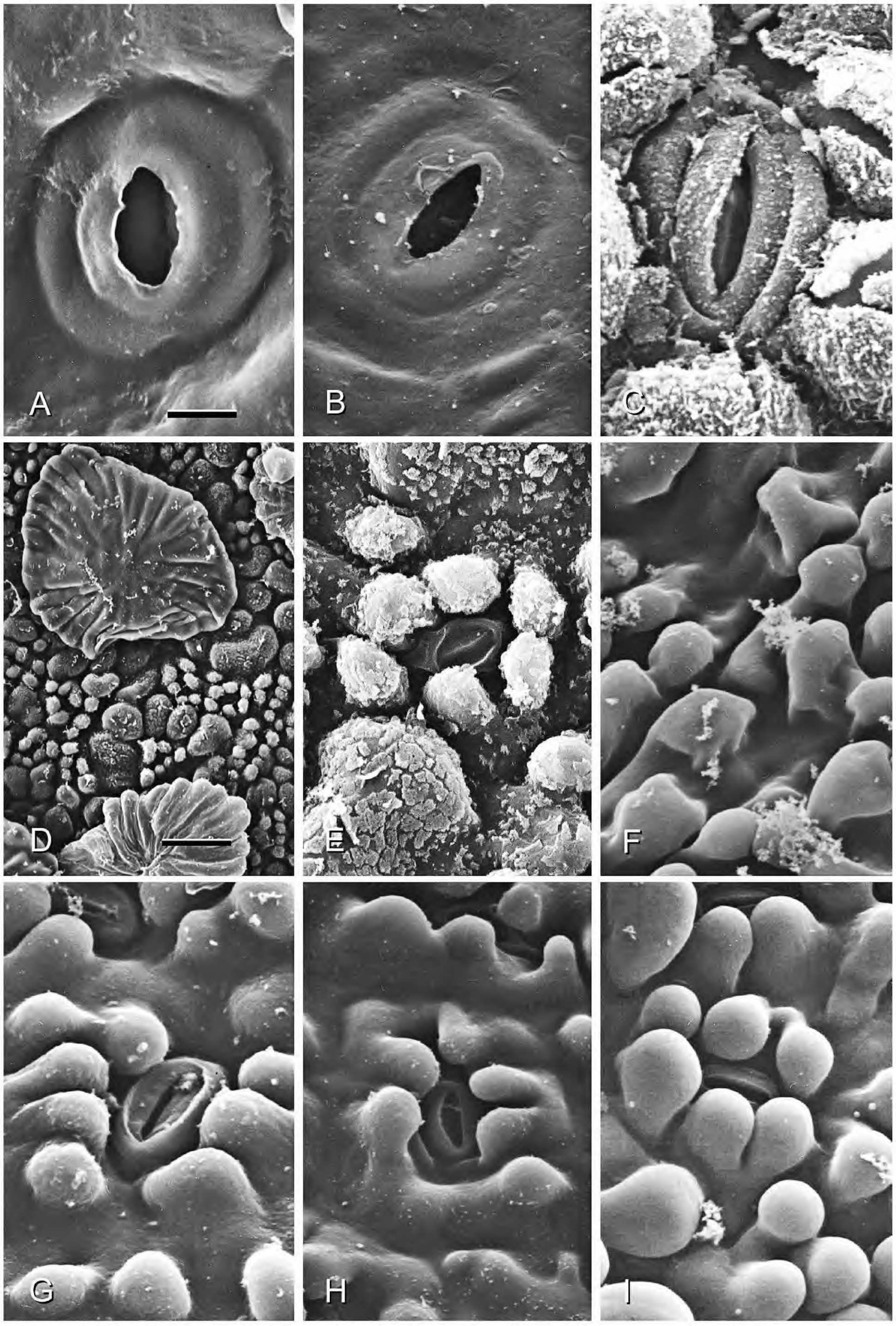

Figure 3. SEM images of abaxial leaf surface of members of the Engelhardioideae. —A. *Engelhardia spicata* Lesch. ex Blume var. *colebrookeana* (Lindl. ex Wall.) Koord. & Valeton (*Tsang 24*) with exposed stomate embedded in a relatively smooth, but undulating epidermis. —B. *Alfaropsis roxburghiana* (Wall.) Iljinsk. (*Clemens 3836*) stomate and epidermal surface similar to Figure 3A. —C. *Oreomunnea pterocarpa* Oerst. (*Stone 1016*) stomate surrounded by five to six wax-encrusted papillae; epidermal surface studded with papillae. —D. *Oreomunnea mexicana* (Standl.) J.-F. Leroy subsp. *costaricensis* D. E. Stone (*Stone 3287*) with stomate partially obscured by epidermal papillae and peltate scales. —E. *Oreomunnea mexicana* subsp. *costaricensis* (*Stone 3287*), devoid of peltate scales to expose stomata with six overarching papillae. —F. *Alfaroa costaricensis* subsp. *costaricensis* (*Stone 2174*) with partially collapsed papillae on the surface of an immature leaf. —G. *Alfaroa*

"from the 19th century until the early 1970s, the expansion of agricultural land was mainly due to the production of export crops [like coffee]."

Historical background. In Manning's 1952 treatment of the Juglandaceae for the *Flora of Guatemala*, *Alfaroa costaricensis* was the only species recognized. We now know, however, that the sterile specimens he referred to as "*Engelhardtia*" *guatemalensis* Standl. are, in fact, *A. guatemalensis* (Standl.) L. O. Williams & Ant. Molina (Williams & Molina, 1970). While dealing again only with sterile specimens, he noted that the status of the Guatemalan *A. costaricensis* is "somewhat uncertain...but the leaves are so closely like those of Costa Rican *Alfaroa* that the Guatemalan tree probably belongs at least to that genus [whereas]...it is to be expected that [the specimens] represent a distinct species" (Manning, 1952: 354). Manning was unable to identify any specific set of characters that could be used to distinguish *Alfaroa* specimens from these two countries. Flowering and fruiting specimens made subsequently in the same general area in western Guatemala, as well as Veracruz (Narave, 1983) and Chiapas, Mexico, now permit a more complete assessment and justification for recognizing northern specimens of *A. costaricensis* as a new subspecies.

Paratypes. GUATEMALA. **Quetzaltenango:** slopes of Volcán Santa Maria, Finca Pirineos, off Hwy. 95 at 197 Km mark, ca. 1600 m, 3 Nov. 1967, *D. E. Stone 2210, 2210A* (DUKE), 18 May 1966, *D. E. Stone 2214, 2214A, 2214B, 2215* (DUKE), 29 May 1971, *D. E. Stone 3015* (DUKE). MEXICO. **Chiapas:** Selva Negra, 10 km from Rayón Mezcalpa along rd. to Jitotol, Mpio. Rayón, 1700 m, 10 Jan. 1981, *D. E. Breedlove & B. T. Keller 49290* (DUKE); 5 km SE of Jitotol, along rd. to Bochil, Mpio. Jitotol, 1600 m, 9 Jan. 1981, *D. E. Breedlove & B. T. Keller 49370* (DUKE), 10 Sep. 1981, *D. E. Breedlove & B. T. Keller 52670* (DUKE). **Veracruz:** Volcán Santa Marta, vertiente W, parte aguas, 1350 m, 16 Mar. 1968, *M. Sousa 3605* (DUKE), 1370 m, 16 Mar. 1968, *M. Sousa 3619* (DUKE).

Synonymy within *Alfaroa manningii*

I described *Alfaroa guanacastensis* D. E. Stone in 1977 as a segregate of *A. manningii* based on perceived differences in their respective leaf and nut morphology (short vs. long leaf petioles, low vs. pronounced ribs on the fruit husk, respectively) and geographic ranges (Pacific vs. Atlantic watershed in Costa Rica). Subsequent collections of these two taxa, as well as a more comprehensive overview of *Alfaroa* throughout Latin America, make a clear distinction between them untenable. It appears now that we are dealing with a series of disjunct populations that are characterized most notably by intergrading differences in sculpture pattern of the fruit husks. Consequently, *A. guanacastensis* is hereby reduced to synonymy under *A. manningii* (León, 1953).

Alfaroa manningii J. León, Ceiba 4(1): 44. 1953, as "*Manningii*." TYPE: Costa Rica. Cartago: Platanillo de Turrialba, 19 July 1951, *J. León 3469* (holotype, CATIE).

Alfaroa guanacastensis D. E. Stone, Fieldiana, Bot. 40: 40, fig. 7. 1977, syn. nov. TYPE: Costa Rica. Apr., *D. E. Stone 2167* (holotype, DUKE; isotypes, A, CR, F, US).

Relationship of *Alfaroa* and *Alfaropsis*

The genus *Alfaropsis* (Iljinskaya, 1993) is most commonly recognized as *Engelhardia roxburghiana* Wall. or *E. chrysolepis* Hance in the monotypic section Psilocarpeae Nagel emend. Leroy (Manning, 1966, 1978). It shares winged fruits with the Old World *Engelhardia* (Jacobs, 1960) and New World *Oreomunnea* (Manning, 1959). *Oreomunnea*, on the other hand, is the closest relative of *Alfaroa* (Manos & Stone, 2001), even though the latter has wingless, drupaceous fruits (Stone, 1977). There has been considerable conjecture as to the validity of recognizing *Oreomunnea* as a distinct genus and its status relative to *Alfaroa* (Manning, 1949; Stone, 1972), since they are virtually impossible to tell apart except for the distinctive pistillate flowers and fruits (Table 2). Support for recognition of Oersted's *Oreomunnea* (1856) was provided by Hjelmqvist (1948, 1960) and Leroy (1951) based on floral morphology, by Stone (1972) emphasizing the fruit and patterns of germination, and subsequently by Manchester (1987) incorporating the fossil history of the fruits. In 1990, Iljinskaya reviewed the taxonomy and phylogeny of the family and concluded, among other things, that *E. roxburghiana* should be treated as a species of *Alfaroa*, namely *A. roxburghiana* (Wall.) Iljinsk. While the evidence for this transfer is a bit confusing, due perhaps in part to our translation from Russian, she did make the case for recognizing this taxon as a link between *Engelhardia* sect. *Engelhardia* and the

←
williamsii (*Stone 3119*) with epidermal papillae surrounding the stomate. —H. *Alfaroa mexicana* (*Stone 2132*) with epidermal papillae surrounding the stomate. —I. *Alfaroa manningii* (*Stone 2220*) with epidermal papillae surrounding the stomate. Scale bars: A–C, E–I = 5.6 μm; D = 33 μm. (N.B. Fig. 3B in Manos & Stone [2001] displays the abaxial leaf surface of *Alfaroa hondurensis* L. O. Williams ex W. E. Manning, but this taxon has subsequently been reduced to synonomy under *A. guatemalensis* [see Stone, in press].)

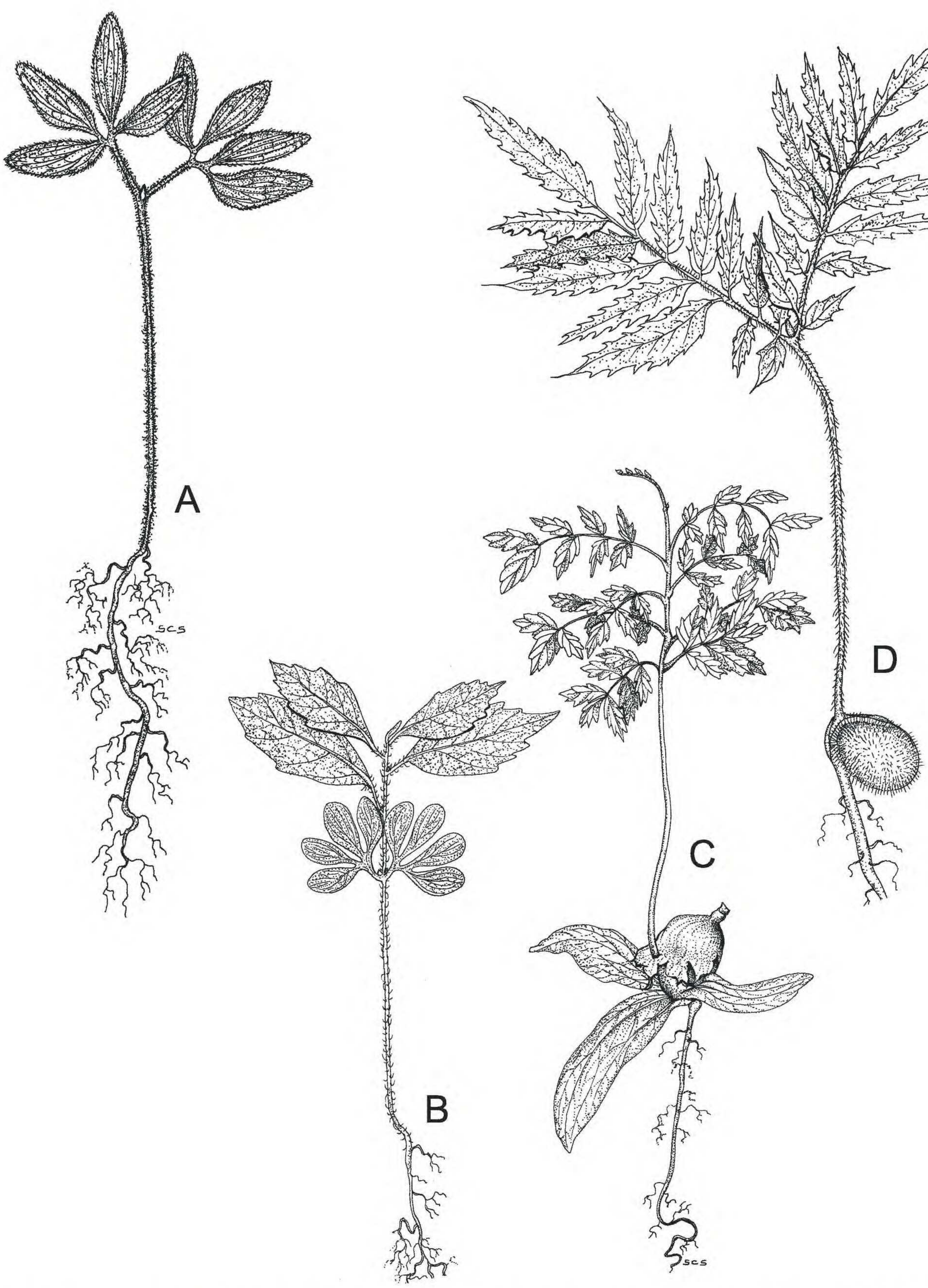

Figure 4. Seedlings of members of the Engelhardioideae. —A. *Engelhardia apoensis* Elmer ex Nagel (*FRI 1299*) with a pair of epigeous cotyledons, deeply bilobed, and each primary lobe further bifurcated (× 0.8). —B. *Alfaropsis roxburghiana* (*M. T. Kao s.n.*) with a pair of epigeous cotyledons similar to Figure 4A and a shoot with the first several leaves simple and alternate (× 0.8) (adapted from Conde & Stone, 1970). —C. *Oreomunnea mexicana* subsp. *mexicana* (*Stone 2142*) with hypogeous cotyledons embedded in a winged fruit and the shoot with opposite, compound leaves (× 0.9). —D. *Alfaroa costaricensis* subsp. *costaricensis* (*Stone 2156*) with hypogeous cotyledons embedded in a thin-skinned nut and shoot with opposite, compound leaves (× 0.5) (adapted from Conde & Stone, 1970).

Alfaroa–Oreomunnea clade (see Manos & Stone, 2001).

Similarities between *Alfaroa roxburghiana* and other members of *Alfaroa* that Iljinskaya contrasted to *Engelhardia* sect. *Engelhardia* include the evergreen habit, androgynous panicles borne terminally on new wood, pollen with a thick nexine, and carinal (split) oriented stigmas (Table 2). Iljinskaya (1993)

subsequently revisited the subject and assessed the characters *A. roxburghiana* shared with *Engelhardia* (e.g., lack of rhombic crystals in the leaf parenchyma, 3-winged fruiting bract that is pinnately veined, 4-chambered fruit, epigeal germination). Her conclusion this time was that *A. roxburghiana* was neither an *Alfaroa* nor *Engelhardia*, but rather deserved recognition at the generic level as *Alfaropsis*. A review of this newly described taxon was not undertaken until Manos and Stone (2001) provided molecular data (i.e., chloroplast DNA and the nuclear ribosomal ITS region) to confirm the distinctness of *Alfaropsis* and its placement as a sister to *Alfaroa–Oreomunnea*. They demurred, however, from formally recognizing *Alfaropsis*, citing the need for a broader sampling of *Engelhardia* species. Although additional molecular evidence has not been forthcoming to date, Manos et al. (2007: fig. 3) included *Alfaropsis* in their discussion of the phylogeny of extant and fossil Juglandaceae.

Whereas the preponderance of evidence would seem to favor recognition of *Alfaropsis* as a distinct clade, there are nevertheless some conspicuous morphological traits that link the genus very closely to the wing-fruited *Engelhardia* (Figs. 3, 4). Prominent here is the structure of the abaxial leaf epidermis that is smooth and undulating in all Old World taxa (Fig. 3A), but papillose in the New World, wing-fruited *Oreomunnea* (Fig. 3C–E) and the nut-fruited *Alfaroa* (Fig. 3F–I). Similarly, seed germination in the Old World *Engelhardia* (Fig. 4A) and *Alfaropsis* (Fig. 4B) is epigeal, whereas the New World *Oreomunnea* (Fig. 4C) and *Alfaroa* (Fig. 4D) have hypogeous cotyledons and hypogeal germination, despite their distinctive differences in the mode of dispersal, namely by wind in *Oreomunnea* and by animal in *Alfaroa* (Stone, 1973).

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